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A DETERMINATION OF THE MAGNITUDE OF THE CELL "SENSITIVE VOLUME" ASSOCIATED WITH THE WHITE-EYE MUTATION IN X-RAYED DROSOPHILA

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Studies of the number of inhibited unicellular organisms in an x-rayed population as a function of total incident or absorbed energy have been made by Crowther,[1] Condon and Terrill,[2] Curie,[3] Glocker,[4] Holweck and Lacassagne,[5] Mayneord,[6] Wyckoff[7] and others. They have led to the estimation of the magnitude of the "sensitive volume," representing the portion of the total cellular content within which incident radiation must be absorbed to be effective. The theory as elaborated by Curie postulates that the observed Poisson distribution of dying organisms in an irradiated population is a consequence primarily of the quantum nature of the "killing" process, rather than of a type of biological variability in the organism. Glocker has satisfactorily verified this conclusion. On this basis, statistical data of the number of individuals "killed" in an irradiated group, as a function of radiation energy, can be so treated as to give information concerning (1) the number of "hits" required to achieve the effect, and (2) the magnitude of the volume or aggregate of volumes in the cell within which a "hit" must occur. It is of peculiar interest to apply this method to a genetic situation.

A study was undertaken of the frequency distribution of the mutation to white eye color in *Drosophila melanogaster* under x-irradiation, as a function of energy input. The extremely low rate of mutation at any single locus, even under x-rays, forbids a study of the mutation rate in germ cells by this method. Patterson[8] has shown that x-rayed larvae of *Drosophila* may at maturity bear mosaic patches of white eye color, composed of somatic tissue arising from single cells of the eye anlage affected at the time of irradiation. The anlage cell rather than the entire organism can thus be made the individual of the experiment, and the probability of inducing the desired mutation in irradiated material is increased owing to the number of cells in the anlage at the time of treatment. Under these con-

ditions, a statistically significant number of mutations can be induced at the white locus.

The stock of *Drosophila* selected was homozygous eosin. Mosaics in the males take the form of white, irregular patches composed of a variable number of ommatidia superposed on the light eosin, male-colored background. The patches may occur on one or both lobes of the eye. Usually but one eye of a given fly is affected. In the female the observed patches, of the same shape and size range as in the male, are composed of light eosin or male-colored ommatidia, superposed on the dark eosin, female-colored background. Patterson has presented good evidence to show that chromosome aberrations in the female result in the production of dark eosin patches, which, against an already dark eosin background, are indistinguishable and therefore not counted. In the male, chromosome aberrations take the form of pits in the eye surface, since they seem to be fatal both to the cell involved and to the ommatidia which would have descended from it. There is little danger with this stock, therefore, of confusing the results of "point-locus" mutations with those of chromosome aberrations. Only data obtained from males are presented here.

A single source of radiation was used, a Coolidge x-ray tube of the "portable" type, air-cooled and with tungsten target, of lead glass equipped with a sodium glass window. It was self-rectifying and was operated directly from a line voltage of 125 v. through a transformer at a potential of 85 kvp. and a current of 10 ma. The distance from the outer surface of the sodium glass window to the upper surface of the irradiated material was kept constant throughout at five inches. The only variable was time of raying. Measurements of the energy incident at the point of exposure of the material were made with a Failla radium-compensated ionization chamber, using a collodion-graphite thimble. The output was found to be 78.1 roentgens per minute, as an average of seven readings taken on two scales of the instrument.

Flies were reared in half-pint milk bottles containing cooked banana-agar medium and inoculated with the Standard Brands "G-M" culture of yeast. Eggs were obtained on drops of the medium on glass squares, which were replaced every six hours. The agar drops were incubated for twenty-four hours from the time of first exposure to the laying flies, when they were irradiated and immediately transferred to fresh culture bottles, where the larvae developed. The eyes of adult flies from irradiated eggs and larvae were examined for mosaic patches with a binocular stereoscopic microscope. Affected eyes were mounted in high-refractive media and studied further.

The following table shows the total number of eyes counted for each x-ray exposure, the number in which whitened facets were discovered, the percentage of the total which these exceptional eyes constituted, and the

percentage probable error of each determination. The percentage error was calculated for each exposure from the formula

$$\text{P.E.} = \pm 0.6745 \sqrt{\frac{p \times q}{n}}$$

where n is the total number of eyes observed, $p = \frac{\text{number of affected eyes}}{n}$ and $q = \frac{\text{number of unaffected eyes}}{n}$. The table refers to data from males only.

EXPOSURE	TOTAL NUMBER	NUMBER AFFECTED	PER CENT AFFECTED	PROBABLE ERROR (PERCENTAGE)
Control	1146	0	0.00	0.000
1/2 Min.	2884	8	0.28	±0.075
1 Min.	2107	11	0.52	±0.106
2 Min.	2114	18	0.85	±0.135
3 Min.	1740	26	1.49	±0.195
4 Min.	320	7	2.14	±0.540

Following the usual analysis applied to killing curves under radiation, a plot may be made of the natural logarithm of the survival ratio against dosage. The shape of the curve will yield information as to the number of "hits" required in the sensitive zone to bring about mutation. If but one electron passage is required the curve will be rectilinear. Higher numbers of "hits" will result in an increasing convexity of the curve. The family of curves for "hit" numbers from one to eleven has been plotted by Curie. When the number of affected individuals lies below ten per cent of the whole, it can be shown to be justifiable to plot instead the percentage of affected individuals against dosage. Such a plot is shown in figure 1, the x-ray dosage being expressed as exposure time, other conditions being constant. It will be seen that the points are best fitted by a straight line, indicating that a single electron passage is sufficient to bring about the mutation. If the assumption be made that *every* electron passing through the locus brings about a mutation, the probability P being thus set equal to 1, a value can readily be derived for the *minimum* volume of the genic locus.

Let N be the total number of individuals considered, and X the number of individuals "hit" in unit time. Then X/N will be the decimal part of individuals hit in unit time.

Let P be the probability that a unit hit will be effective (= 1 for this case).

$$\text{Let } \delta = \frac{\text{ion pairs produced}}{\text{cc./min.}} = \frac{r/\text{min.}}{4.77 \times 10^{-10} \times 1.2 \times 10^{-3}}$$

where r is the x-ray dosage in roentgens.

Let Q be the rate of absorption of quanta by the "sensitive volume" =

$V\delta$ for fairly soft radiation, where V is the "sensitive volume." Expressing the rate of change of X with time as $\frac{dX}{dt} = NQP$, or $dX = NQPdt$ and integrating, $X = NQPt$, and $X/N = QPt$. Since $Q = V\delta$, $X/N = V\delta Pt$, and

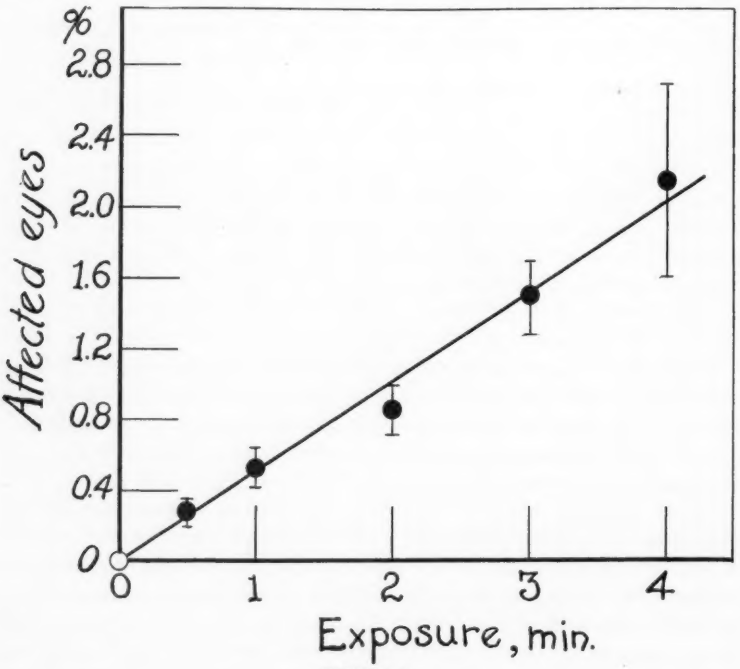

FIGURE 1

Plot of percentage of mutant eyes as a function of x-ray energy input. The data represented are for male individuals only. The vertical lines indicate the magnitude of the percentage probable error for each determination.

$V = (X/N)/\delta Pt$ and P drops out ($P = 1$). Substituting the value of δ already given,

$$\text{Sensitive Volume} = \frac{\frac{\%\ \text{Affected Individuals}}{100}}{\frac{r/\text{min.} \times t}{4.77 \times 10^{-10} \times 0.0012}}$$

It is understood that this form of calculation may be applicable only in an order-of-magnitude determination of genic size, to which it is here applied, within the wave-length range of the radiation used.

Consider the form of the calculation for the data given earlier for the one-half minute exposure:

Here $t = {}^1/_2$ min., $r = 78.1$ r/min., $X/N = 0.00280$.

Then

$$V = \frac{\dfrac{280 \times 10^{-5}}{78.1 \times 10^{-5}}}{4.77 \times 10^{-10} \times 1.2 \times 10^{-3}} = 41.04 \times 10^{-18} \text{ cc.}$$

Similar calculations from the data obtained at other exposures yield values of 38.11×10^{-18} cc., 31.15×10^{-18} cc., 36.40×10^{-18} cc. and 39.21×10^{-18} cc. for irradiation times of one, two, three and four minutes, respectively. The weighted mean of these values calculated according to the percentage error of the observations is 37.06×10^{-18} cc. This number may be interpreted to represent the lower limiting value of the total volume of the white loci in the X-chromosomes of all cells of the optic anlage at the time of treatment.

It remains to ascertain the number of cells present in the anlage at this time. Work is in progress to determine this number cytologically. The average of the quotients of the number of whitened to the total number of ommatidia in several eyes may at present be taken as a useful index of the order of magnitude of the average number of cells present in the anlagen of larvae of the age-group which was irradiated (eighteen to twenty-four hours from the time of fertilization of the ova). This average ratio for thirty-nine affected eyes was found to be 19.96, indicating the number of cells present to have been of the order of magnitude of twenty. Hersh's[9] value of 750 for the mean number of facets in the normal *Drosophila* eye was used in this calculation for the determination of the number of facets involved.

With this assumption, the individual genic volume was calculated as 1.85×10^{-18} cc. The corresponding radius, assuming the gene to be spherical in form, will be 7.62×10^{-7} cm. for males.

It is interesting to compare these values with those obtained by other workers using other methods. Morgan[10] obtained values of $2.0 \times 10^{-2} - 6.0 \times 10^{-2}$ as upper limits of the radius of the average single gene in *Drosophila*. Blackwood[11] obtained $2.5 \times 10^{-3}\mu - 4.0 \times 10^{-3}\mu$ as minimum values. Gowen and Gay[12] calculated linear dimensions of $3.9 \times 10^{-4}\mu$ and $5.0 \times 10^{-2}\mu$ for the average of a class of genes, assuming them to be of unsymmetrical form, which would yield a value of $1.0 \times 10^{-2}\mu$ on a side, or a radius of approximately $5.0 \times 10^{-3}\mu$, on the assumption of radial symmetry. The present value of $7.62 \times 10^{-3}\mu$ for the gene for white eye color is bracketed within the range covered by these values.

Further work is in progress, and a more detailed account will soon be published.

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[1] Crowther, J. A., *Proc. Roy. Soc.*, **B96,** 202–210 (1924); *Ibid.*, **100,** 390–404.

[2] Condon, E. U., and Terrill, H. H., *Jour. Cancer Res.*, **11,** 324–333 (1927).

[3] Curie, M., *Compt. rend.*, **188,** 202–204 (1929).

[4] Glocker, R., *Naturwiss.*, **19,** 20 (1931); *Zeits. Physik.*, **77,** 653–675 (1932).

[5] Holweck, F., *Compt. rend.*, **186,** 1318–1319 (1928); *Ibid.*, **188,** 197–199 (1929); *Ibid.*, **190,** 527–529 (1930). Holweck, F., and Lacassagne, A., *Compt. rend. soc. biol.*, **100,** 1101–1103 (1929).

[6] Mayneord, W. V., *Proc. Roy. Soc.*, **A130,** 63–80 (1931); *Ibid.*, **A146,** 867–879 (1934).

[7] Wyckoff, R. W. G., *Jour. Exptl. Med.*, **52,** 435–446 (1930); *Ibid.*, **52,** 769–780 (1930); *Jour. Gen. Physiol.*, **15,** 351–361 (1932). Wyckoff, R. W. G., and Rivers, T. M., *Jour. Exptl. Med.*, **51,** 921–932 (1930).

[8] Patterson, J. T., *Jour. Exptl. Zoöl.*, **53,** 327–372 (1929).

[9] Hersh, A. H., *Sci.*, **80,** 547 (1934).

[10] Morgan, T. H., Bridges, C. B., and Sturtevant, A. H., *The Genetics of Drosophila.*

[11] Blackwood, O., *Phys. Rev.*, **37,** 1698 (1931).

[12] Gowen, J. W., and Gay, E. H., *Genetics*, **18,** 1–31 (1933).

FURTHER DATA ON MATERNAL EFFECTS IN DROSOPHILA PSEUDOÖBSCURA HYBRIDS

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Race *B* females of *Drosophila pseudoöbscura* crossed to race *A* males produce sterile F_1 hybrid males having visibly small testes. The reciprocal cross, $A\,♀ \times B\,♂$, produces in F_1 sterile males that have testes of normal size. One of us[1] has shown that this difference between the reciprocal crosses is due to a maternal effect. Before fertilization, the cytoplasm of the eggs deposited by race *B* females is so influenced by the chromosomes present in it, that an interaction between this cytoplasm and the autosomes of race *A* (introduced by the spermatozoon) results in the development of small testes in males arising from such eggs. On the other hand, the cytoplasm of an *A* race egg is so determined by the maternal chromosomes, that the introduction of *B* race autosomes results in development of large

testes. That a maternal effect, and not plasmatic inheritance, is involved in this case is proved by the fact that the further generations of the hybrids (obtained by back-crossing F_1 hybrid females to males of either parental race) are alike, irrespective of whether they carry race *A* or race *B* cytoplasm. In the present note we wish to report some further experiments bearing on the problem of maternal effects versus plasmatic inheritance.

Race *A* females carrying the second chromosome dominant Bare were crossed to race *B* males homozygous for the second chromosome recessive cinnabar. F_1 females were back-crossed to cinnabar, cinnabar females selected in the next generation and further back-crossed to cinnabar males from the original cinnabar stock for four more generations. A cinnabar stock was thus established which presumably has all chromosomes of race *B*, but whose cytoplasm is ultimately derived from the race *A* ancestor. Cinnabar flies from this stock are fertile in both sexes. To test whether the race *A* cytoplasm has any effects on the properties of these flies, such cinnabar females were crossed to wild-type race *A* males, and the size of the testes in the F_1 hybrid males was measured. As a control, cinnabar females from the original cinnabar stock (i.e., having race *B* cytoplasm) were crossed to race *A* males from the same strain as above. This test is very sensitive, since testis size in the F_1 hybrid males from the cross $B♀ \times A♂$ is highly variable, and different strains of race *A*, as well as of race *B*, give quantitatively very different results.[2] The length of the testis in the males from the experimental and the control cultures is given below (in μ):

	$M \pm m$	σ	Limits	n
Race *A* cytoplasm	401.2 ± 5.6	56.0	278–557	100
Race *B* cytoplasm	393.9 ± 7.0	70.1	261–557	100

The difference between the two mean values is clearly non-significant, being smaller than its standard error. Another similar experiment was arranged by crossing and back-crossing race *A* Bare females to wild-type race *B* males (from the Seattle-4 strain) for five generations. A wild-type strain was thus obtained that should have all or most chromosomes from the race *B* Seattle-4 strain, but the cytoplasm of race *A*. Females from this strain were crossed to race *A* males. As a control, females from the original Seattle-4 strain were crossed to the same race *A* males. Testis size in the F_1 hybrids was found to be (in μ):

	$M \pm m$	σ	Limits	n
Race *A* cytoplasm	250.6 ± 4.6	4.58	122–365	100
Race *B* cytoplasm	246.7 ± 4.4	4.38	157–365	100

Testis size is again independent of the ultimate source of the cytoplasm. The difference between the testis size in the two pairs of experiments is due to the fact that the Seattle-4 strain is a "strong" *B* race, while cinnabar is a "weak" *B* race.[2]

Race *A* females carrying Bare were crossed to race *B* males homozygous for the third chromosome recessive orange. In each of the succeeding fourteen generations Bare non-orange females were selected, and backcrossed to orange males from the orange strain. Wild-type, Bare, orange and Bare orange flies appear in each generation. The strain thus obtained produces flies that have all *B* race chromosomes, except that some of them (those showing Bare) retain the section of the race *A* second chromosome carrying the locus of Bare, and some (those that are non-orange) retain the section of the race *A* third chromosome containing the locus of the wild-type allelomorph of orange. The testis size in the males in the fourteenth generation is as follows (in μ):

	$M \pm m$	σ	Limits	n
Wild-type	582.0 ± 10.6	106.5	278–748	100
Orange	514.3 ± 7.9	78.6	278–661	100
Bare	371.0 ± 10.1	101.3	192–626	100
Bare orange	322.2 ± 8.6	86.3	157–592	100

Normal males of race *B* of *Drosophila pseudoöbscura* have in similar culture conditions average testis size above 600μ, and only seldom individual males are found having testis length below 450μ. All four classes of males have, thus, testes smaller than normal. Those carrying Bare are invariably sterile, the non-Bare ones frequently so. The sterility of the Bare males shows that the section of the second chromosome of race *A* including the locus of Bare carries also a gene, or genes, whose presence in the race *B* genotype is incompatible with fertility of the males. The orange males carry, however, only race *B* chromosomes, and hence should have testes of normal size, and should be normal in fertility. This is not the case. Since, as shown above, the cytoplasm has *per se* no effect on testis size or fertility, the reduction of the testis size in the orange males must be due to a maternal effect. The presence, in a female having mostly race *B* chromosomes, of the portion of the race *A* second chromosome carrying the locus of Bare (or the portion of the race *A* third chromosome carrying the wild-type allelomorph of orange or perhaps the simultaneous presence of these two sections) modifies the cytoplasm of the eggs deposited by such a female in such a manner that the males developing from these eggs have testes smaller than normal in size even if they carry only race *B* chromosomes. The fact that no lasting or permanent modification of the properties of the cytoplasm is thus produced is, however, demonstrated by the following experiment. Orange non-Bare daughters of Bare females were crossed to orange males. All males produced in the next generation had testes of normal size. It is also established that not every section of *A* race chromosomes present in *B* race genotype produces a maternal effect. For instance, females having *B* race chromosomes except for the section of the X-chromosome carrying Pointed produce, when crossed to race *B* males, two kinds

of sons: Pointed and non-Pointed ones. The former have small testes and are sterile, the latter have normal testes and are fertile.

The offspring of the F_1 hybrid females back-crossed to males of one of the parental races consist of individuals having different combinations of the parental chromosomes. Among the males in this offspring, some have large testes and are at times fertile, others have intermediate or small testes and are sterile. It can be shown that males having all or most chromosomes of the same race have large testes, and those having a mixture of the chromosomes of both races have small testes, the smaller the more mixed are the chromosomes. However, in certain backcrosses to race *B* a paradoxical result was obtained: males possessing exclusively race *B* chromosomes had smaller testes than males having once race *A* third chromosome in otherwise race *B* genotype. This result was shown to be independent of the ultimate source of the cytoplasm, i.e., backcrosses having a race *A* grandmother behaved just as backcrosses having a race *B* grandmother did. Two explanations of this result may be suggested. First, the presence of a single race *A* third chromosome in a predominantly race *B* genotype is *per se* favorable for the testis development. Second, the race *A* third chromosome increases testis size in the males having mostly race *B* chromosomes only provided these males develop from eggs deposited by a hybrid female (which, of course, has half of chromosomes from race *A*, and the other half from race *B*). This alternative may be tested experimentally. The back-cross females having all *B* race chromosomes except one race *A* third were crossed to pure race *B* males. The experiment was so arranged that in the offspring the individuals having all race *B* chromosomes could be distinguished from those having a race *A* third by their phenotypes. Such an experiment showed that in the second back-cross generation largest testes are present in males having exclusively race *B* chromosomes. Hence, here again we are dealing with a maternal effect.[3]

It has been known for some time[4] that in the offspring of the first back-cross to either race the sex ratio is abnormal in favor of females. To this should be added that many of the back-cross flies, especially among the males, are weak, visibly abnormal, and in general deficient in vigor. Females are frequently sterile. This condition contrasts with that observed in the first generation of hybrids, where the flies are more nearly as vigorous as the non-hybrid flies; the F_1 hybrid males are all sterile, but females seldom fail to produce some offspring. The following observation throws, perhaps, some light on the situation. If the chromosomes of parents are marked by mutant genes that produce no striking decrease of viability either in the pure races or in the F_1 hybrids, the back-cross hybrids, especially the males, show the Mendelian ratios for these genes grossly distorted. It appears then, that factors producing little, if any, decrease of viability in the pure races or in F_1 hybrids have a considerable deleterious

effect in the first backcross. The important point is, however, that this deleterious effect is manifested not in flies that have a particular combination of race *A* and race *B* chromosomes, but in all back-cross flies. Indeed, the classes having a given combination of race *A* and *B* chromosomes may be practically inviable with one set of marking genes, and may be represented by numerous individuals with another set of markers. The situation is best explained by assuming that the development of eggs of hybrid females is somehow disturbed by the hybrid chromosomes they carry before fertilization, and the individuals developing from these eggs are less able to withstand the effects of unfavorable factors than normal flies. In the experiments thus far done mutant genes known only in race *A* had on the whole a more unfavorable effect on the hybrids than race *B* mutants. Since, however, relatively few genes of either kind were tested, not much weight should be attached to this generalization.

As pointed out by Poulson,[5] the time of development of the reciprocal hybrids in *Drosophila pseudoöbscura* shows probably a maternal effect too. Poulson found that the larval, and especially the pupal, development of race *B* is longer than in race *A*. The time of development of the $A\,♀ \times B\,♂$ hybrids is more nearly similar to that in race *A*, while the development of the $B\,♀ \times A\,♂$ hybrids is more similar to that in race *B*.

Five more or less clear cases of maternal effects are, thus, established in the interracial hybrids of *Drosophila pseudoöbscura*. This number seems high as compared with the situation in *Drosophila melanogaster*, where, in spite of the incomparably larger amount of genetic work done on the latter species, only a few clear cases of maternal effect are known. Whether or not this difference between *pseudoöbscura* and *melanogaster* is real, and if so what is the cause of it, remains at present a matter of speculation.

[1] Dobzhansky, Th., "Maternal Effect as a Cause of the Difference between Reciprocal Crosses in *Drosophila pseudoöbscura*," These PROCEEDINGS, **21**, 443–446 (1935).

[2] Dobzhansky, Th., and Boche, R. D., "Intersterile Races of *Drosophila pseudoöbscura*," *Biol. Zbl.*, **53**, 314–330 (1933).

[3] Experiments referred to in this paragraph will be described in more detail in a separate publication.

[4] Lancefield, D. E., "A Genetic Study of Two Races or Physiological Species in *Drosophila obscura*," *Zeit. ind. Abst. Vererbgsl.*, **52**, 287–317 (1929).

[5] Poulson, D. F., "Times of Development of the Two Races of *Drosophila pseudoobscura*," *Jour. Exp. Zoöl.*, **68**, 237–245 (1934).

OCCURRENCE OF LOWER OLIGOCENE MAMMAL-BEARING BEDS NEAR DEATH VALLEY, CALIFORNIA

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Introduction.—It is a curious fact that while the White River deposits with their wealth of vertebrate fossils are widely distributed in the western Great Plains and occur also in certain of the intermontane basins of the Cordilleran province, no horizon, recognized on the basis of land mammals as equivalent in time to the lower Oligocene or Titanotherium Zone, has been found beyond these areas on the North American continent.[1] All the more unusual does this fact seem when it is realized that since the definition of the White River Group by Hayden in 1862 and the early researches on the White River fossil vertebrates by Leidy, Cope and Marsh, field investigations in the Tertiary have progressed broadly and intensively over the Far West.

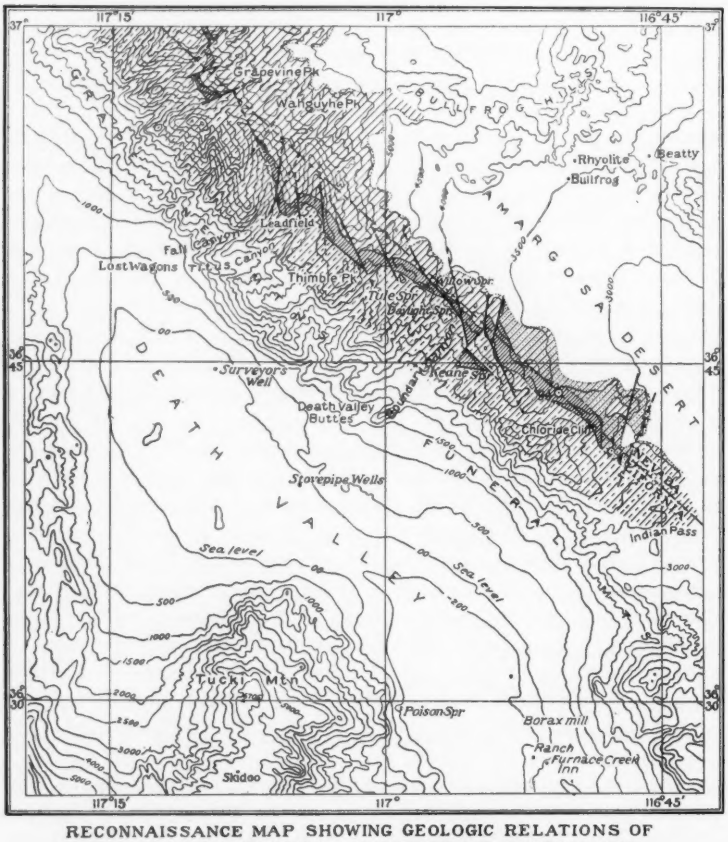
Discovery of a significant record of this stage of the Oligocene in the Amargosa range, adjacent to Death Valley, not only brings a welcome addition to our knowledge of the distribution and relationships of lower Oligocene faunas, but also possesses important implications with regard to the early Tertiary history of this portion of the western Great Basin.

The region, due in large measure perhaps to its inaccessibility and desolateness, has received in the main only reconnaissance study. However, the early investigations of the geology of the Grapevine and Funeral Mountains by Gilbert,[2] Spurr and by Ball elucidated much important information as part of the noteworthy contributions made by these surveys to an understanding of the stratigraphy and structure of southern Nevada and eastern California.

Credit for the discovery of vertebrate fossils in the Tertiary series of the Grapevine and Funeral Mountains goes to H. Donald Curry, former graduate student in the Division of Geology and Paleontology at the California Institute and more recently Acting Ranger-Naturalist at the Death Valley National Monument. During the fall of 1934, Mr. Curry, while traveling over the little-used road between Rhyolite, Nevada, and the now deserted mining camp of Leadfield in Titus Canyon, Grapevine Mountains, saw and collected, in an outcrop of maroon or chocolate-colored, calcareous mudstones exposed in the face of a road-cut, a portion of a titanothere jaw with teeth. Later, excavations at this locality (Locality 253 Calif. Inst. Tech. Vert. Pale.) revealed additional lower jaw material as well as a splendidly preserved skull of a titanothere. Subse-

quent investigations conducted by field parties from the California Institute have been generously permitted by the National Park Service.

History of Geologic Studies in Region.—The first detailed description of



RECONNAISSANCE MAP SHOWING GEOLOGIC RELATIONS OF TITUS CANYON FORMATION IN GRAPEVINE AND FUNERAL MTS.

PLIOCENE? *Tuffs, shales and sandstones*

LOWER MIOCENE? *Undifferenciated rhyolites and tuffs*

LOWER OLIGOCENE (Titus Canyon formation) *Red and green conglomerates, calcareous sandstones, mudstones and tuffaceous sandstones*

PALEOZOIC AND PRE-PALEOZOIC *Limestones, quartzites and shales*

Scale 5 0 5 10 MILES

Contour interval 500 feet

PLATE 1

Tertiary sediments in southwestern Nevada was made by H. W. Turner[3] in 1900. Turner described a succession of conglomerates, sandstones, tuffs and associated flows of rhyolite and andesite in the vicinity of the

Silver Peak Range, 100 miles northwest of the Grapevine Mountains, and named the series the Esmeralda. The basal beds of the series were found to lie unconformably on Paleozoic rocks. Although a probable Miocene age was given to the series, it was recognized that a range in age from Eocene to Pliocene might well be represented.

Spurr[4] in the same year referred the Esmeralda to the late Eocene or early Miocene because part of this series occurs beneath the oldest rhyolite in the Silver Peak Range, which he regarded as of Eocene age. Three years later Spurr[5] described the sediments occurring along the east side of the Amargosa Range and in Death Valley, referred them to the Esmeralda, and reiterated his earlier statement that this formation is late Eocene to early Miocene in age. In 1905 Spurr[6] described the Siebert Tuff at Tonopah, Nevada, and referred this deposit to the middle or late Miocene, distinguishing it from the Esmeralda, which he regarded as older.

In 1907 Ball[7] gave a more detailed description of the Tertiary sediments on the east side of the Amargosa Range and in Death Valley. Ball noted that conglomerates exposed in the vicinity of Boundary Canyon contained boulders of rhyolite. Believing that these boulders were derived from an early Miocene rhyolite, exposed in the immediate vicinity, Ball referred the conglomerates to the middle Miocene and correlated them, as well as the borax-bearing sediments in Death Valley with the "Siebert Lake Beds," the Siebert Tuff of Spurr. In reality, however, the rhyolite boulders in the vicinity of Boundary Canyon have their origin in rocks belonging to an older period of vulcanism, and the sediments in this area observed by Ball are older than and lie beneath his early Miocene rhyolites.

Occurrence.—The sedimentary series containing fossil vertebrates outcrop in a narrow, almost continuous, belt along the eastern side of the Grapevine and Funeral Mountains. Position of this belt coincides roughly with the California-Nevada state boundary in this region and extends from a point a few miles northwest of Grapevine Peak southeasterly to a point approximately five miles southeast of Chloride Cliff. The beds comprise quartzite conglomerates, sandstones, calcareous mudstones, algal limestones and tuffaceous sandstones. At the base is a limestone breccia. This series of sediments is here designated the *Titus Canyon formation*, from its typical occurrence in Titus Canyon near Leadfield, California. The Titus Canyon formation dips in an E to NE direction off the east flank of the Grapevine and Funeral Mountains and lies with marked unconformity upon Paleozoic sediments, frequently with a strike nearly at right angles to the structure discerned in the older rocks. It is overlain unconformably by 400–500 feet of conglomerate, which is interbedded with and lenses upward into rhyolite flows unquestionably the correlative of Rhyolite No. 1, the lowermost volcanic flow recognized by Emmons and Garrey in the Bullfrog Hills, Nevada. In the vicinity of Titus Canyon

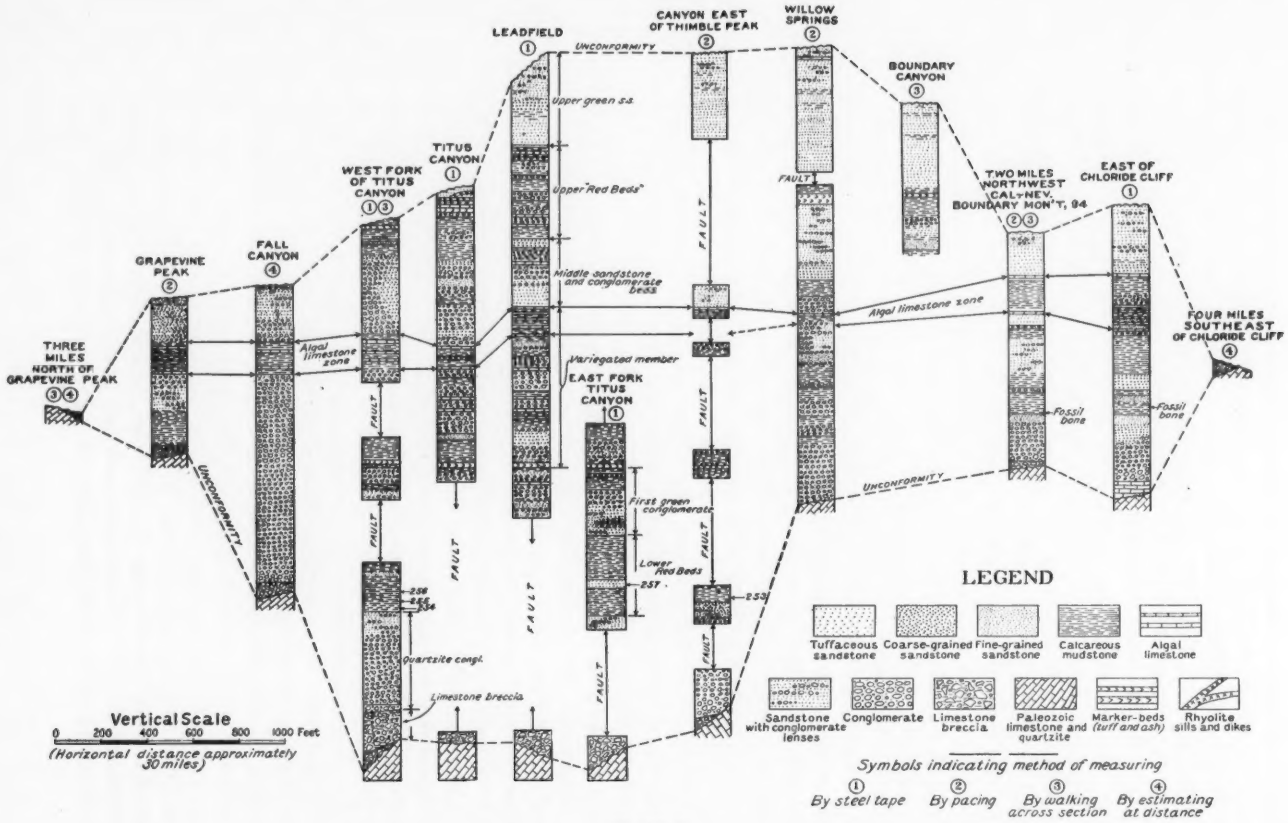


PLATE 2

Columnar sections of lower Oligocene Titus Canyon formation in Grapevine and Funeral Mountains, California. Nos. 253–257 refer to Calif. Inst. Tech. Vert. Pale. Coll. localities.

these volcanics and associated sedimentary tuffs have a total thickness of more than 7000 feet.

The stratigraphic succession of lithologic types is indicated in the columnar sections on the accompanying chart. Outcrops of the basal limestone breccia show angular blocks of Paleozoic rocks like those now exposed in the Paleozoic section immediately to the southwest. Angular blocks of limestone near the base of this member occasionally have a diameter of nearly 20 feet. Laterally, the limestone breccia thickens and thins rapidly and field evidence indicates apparently that it filled depressions in the surface on which the Titus Canyon formation was deposited. The poor sorting, frequent large size and angularity of constituent boulders indicate that the source of this material was not far away. The upper part of this member contains a few well rounded quartzite boulders and grades upward into the quartzite conglomerate. In texture, the limestone breccia resembles most closely recent talus material found in the vicinity of limestone cliffs. While it is difficult to recognize the extent of lateral variation in a direction normal to the strike of the sediments, the limestone breccia is seen to pinch out southwesterly under the quartzite conglomerate on the northwest wall of Titus Canyon.

The general character of the quartzite conglomerate and of all overlying conglomerates is that of fluviatile gravels. The conglomerates contain an abundance of well rounded, highly polished, quartzite boulders. Limestones are common and, it is important to note, that rhyolite, granite and quartz monzonite boulders are present although rare. The thickness and lithology of the calcareous mudstones and algal limestones are rather constant along the strike. Consequently these beds make excellent stratigraphic markers. In the middle part of the section, the succession of deposits is markedly irregular. Frequently an algal limestone bed is found intercalated in two thick strata of coarse conglomerate.

A distinctive horizon of yellow and blue-gray algal limestones and of red or maroon, calcareous mudstones near the upper middle of the section has been termed the Algal Limestone Zone. This zone occurs but once in every section measured along the lateral extent of the deposits. Its characters are so distinctive and constant as to preclude the possibility of confusion with sediments elsewhere in the stratigraphic sequence. For this reason the beds, although now encountered in discrete sections on individual fault blocks, are regarded as having accumulated simultaneously throughout the area, and correlation of the various sections has been made largely on the basis of position of this zone.

The upper part of the section in Titus Canyon consists of red conglomerates and red and green calcareous mudstones, overlain by massive, usually well sorted, green, tuffaceous sandstones and pebble conglomerates. The uppermost member of this group is present only in the region between

Columnar sections of lower Oligocene Titus Canyon formation in Grapevine and Funeral Mountains, California. Calif. Inst. Tech. Vert. Pale. Coll. localities.

PLATE 3A

PLATE 3B

(Description of Plate 3 on opposite page.)

Titus and Boundary Canyons. Elsewhere it has been removed by erosion prior to the extravasation of the rhyolites. The green tuffaceous sandstones at the top of the section east of Chloride Cliff have been correlated with a similar unit in Titus Canyon, immediately overlying the algal limestone zone, rather than with the uppermost green sandstones, on the basis of position of this zone in the Chloride Cliff section.

A distinct angular discordance is present between the Titus Canyon formation and the overlying conglomerates and associated rhyolites northwest of Leadfield as well as at the top of the section in Titus Canyon. A similar angular discordance is seen in the area east of Chloride Cliff where the overlying volcanics cut across the Titus Canyon formation and rest directly on pre-Tertiary rocks. At other localities, however, no angular discordance has been observed. Correlations by means of the algal limestone zone indicate that in the vicinity of Grapevine Peak and Chloride Cliff more than 1000 feet of the upper part of the Titus Canyon formation was removed prior to deposition of the rhyolites and accumulation of their basal conglomerate. Presence in the overlying conglomerates of boulders derived from the underlying Titus Canyon also favors existence of an unconformity. Localization of an angular discordance suggests that prior to accumulation of the overlying rhyolite the area was compressed in a north-south direction, causing local folding with development of axes normal to this direction and an elevation of the northern and southern ends of the region to an extent sufficient to allow the removal of 1000 feet of sediments in these areas. A few small faults were found extending up to, but not cutting the contact above, the Titus Canyon formation.

Fauna and Age.—Fossil mammalian remains have been found in the lower portion of the Titus Canyon formation where they usually occur in red calcareous mudstones. All of these occurrences are below the algal limestone zone. The fauna comprises the horse, *Mesohippus*, titanotheres representing presumably two types, hyracodont rhinoceroses, several distinct types of artiodactyls including the genus *Agriochoerus*, and a sciuromorph rodent. The titanotheres, in stage of evolution, are more nearly related to the genera *Brontops*, *Brontotherium* and *Menodus*,

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DESCRIPTION OF PLATE 3

A. View of Titus Canyon formation in area east of Chloride Cliff, Funeral Mountains, California. Unconformable contact with overlying conglomerates parallels skyline in right background.

B. Exposures of Titus Canyon formation in vicinity of Leadfield, Grapevine Mountains, California. Basal limestone breccia lies on Paleozoic rocks seen in right wall of canyon. Lower red beds concealed beneath alluvium of canyon bottom; middle and upper parts of section exposed on mountain face at left. Overlying volcanics form left sky-line. Difference in elevation between top of mountain on left and canyon bottom is more than 3000 feet.

known from the Titanotherium Beds of the White River group, than to Eocene types. The hydracodont rhinoceroses may represent types more primitive than those recorded from the White River. The Titus Canyon fauna is certainly later in age than the Duchesne River assemblage and the Uppermost Eocene fauna recorded from the Sespe of California, and is earlier than the Oreodon and Leptauchenia zones of the White River. Characters exhibited by the titanotheres and presence of *Mesohippus* furnish the principal evidence for recognition of a close age relationship between this horizon and the Titanotherium Zone. Since the latter has been generally regarded as belonging to the lower Oligocene, this age may likewise be assigned to the Titus Canyon formation.

Concluding Remarks.—Discovery of a fossil vertebrate fauna in the Grapevine Mountains and recognition of the Titus Canyon formation in which this assemblage occurs, has considerable significance in that (1) lower Oligocene land mammals are recorded for the first time in the Great Basin Province and far from previously known areas of occurrence, and (2) a definite age determination can be made for the lowermost formational unit in the Tertiary rock sequence of the Grapevine and Funeral Mountains.

Further, since the basal limestone breccia of the Titus Canyon formation consists of material which has undergone little transportation and has been derived from Paleozoics in the immediate vicinity and since prevailing dips on planes of cross-bedding in the sandstones and conglomerates are toward the northeast, the suggestion is strongly given that the material comprising the Titus Canyon formation was derived from rocks exposed not far to the west. Presence of algal limestone beds in the upper portion of the formation indicates that some of the deposits accumulated in standing water. The conglomerates, however, appear to have been deposited under fluviatile conditions.

Present evidence seems to indicate that the basal part of the lower Oligocene formation accumulated along the flanks of a mountain range the position of which was somewhat like that of the present Grapevine and Funeral Mountains. Following an accumulation of sediments sufficient to bury many of the irregularities of the pre-existing land surface below the Titus Canyon formation, lacustrine conditions prevailed. The deposition of algal limestones and calcareous mudstones was, however, frequently interrupted by an introduction of coarser sediments carried in by streams from the bordering range. Determination of these lower Oligocene topographic features for an area that roughly coincides with a region displaying similar land forms at the present time suggests an age for the present Basin Range topography in at least this portion of the Great Basin.

[1] Recent studies by Stock (see *Proc. Nat. Acad. Sci.* 1932–1935) have shown the presence of an uppermost Eocene mammalian fauna in the Sespe deposits, north of the Simi

Valley, Ventura County, California. In the history of North American mammal life this fauna has a position immediately antecedent to that of the Titanotherium Zone. Above this stage in the Sespe is a considerable thickness of land-laid material and some of these deposits are without much doubt lower Oligocene in age although in the absence of fossil remains this cannot be definitely proved at the present time.

[2] Gilbert, G. K., *U. S. Geog. Surv. West 100th Mer., Wheeler Surv.*, **3**, 33 (1875).

[3] Turner, H. W., *U. S. Geol. Surv. 21st Ann. Rpt.*, Pt. 2, 197–208 (1900).

[4] Spurr, J. E., *Jour. Geol.*, **8**, 633 (1900).

[5] Spurr, J. E., *U. S. Geol. Surv. Bull.*, **208**, 19, 185 (1903).

[6] Spurr, J. E., *U. S. Geol. Surv. Prof. Pap.* **42**, 51–70 (1905).

[7] Ball, S. H., *U. S. Geol. Surv. Bull.*, **308**, 32–34, 165–166 (1907).

ADOPTION OF THE METER-KILOGRAM-MASS-SECOND (M.K.S.) *ABSOLUTE SYSTEM OF PRACTICAL UNITS BY THE INTERNATIONAL ELECTROTECHNICAL COMMISSION* (I.E.C.), *BRUXELLES, JUNE, 1935*

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At its plenary meeting in June, 1935, in Scheveningen-Bruxelles, the I.E.C. unanimously adopted the M.K.S. System of Giorgi, as a comprehensive absolute practical system of scientific units.

The last preceding international action of a similar character was in 1881, when the International Electrical Congress of Paris[1] adopted the centimeter-gram-second (C.G.S.) system.

Commencing with that action in 1881, various International Electrical Congresses, up to that of 1893 at Chicago,[2] and since then, the I.E.C.,[3] have adopted, by successive steps, the well-known series of nine practical electromagnetic units (*ohm, volt, ampere, farad, coulomb, joule, watt, henry* and *weber*). These practical units are recognized as not pertaining to the C.G.S. system; but as being derived therefrom through a corresponding series of decimal multiples (10^9, 10^8, 10^{-1}, 10^{-9}, 10^{-1}, 10^7, 10^7 and 10^8). It was pointed out by Clerk-Maxwell,[4] that the series might be considered as belonging to a practical absolute system having for its fundamental units the length of an earth-quadrant, (10^9 cm.), the mass of an eleventh-gram (10^{-11} g.) and the mean solar second of time (Q.E.S.). In the Q.E.S. system, the numerical value of μ_0 space permeability, was unity, the same as in the C.G.S magnetic system. The units of length and mass in the Q.E.S. system are so awkward that neither Maxwell, nor any unitologist since his time, has ever seriously proposed the practical adoption of the Q.E.S. system. It has remained an academic curiosity.

In 1901, however, Prof. G. Giorgi of Rome[5] showed that if the numerical

value (rationalized) of space permeability μ_0 were taken* as $4\pi \times 10^{-7}$, the entire series of electromagnetic practical units could be considered as belonging to a new practical absolute system, having as unit of length the international meter of Sèvres, as unit of mass the international kilogram of Sèvres and as unit of time the mean solar second. Prof. Giorgi communicated a paper on the subject of his proposed system to the International Electrical Congress of St. Louis, in 1904.[6] The proposal gradually received support from physicists and engineers, until it was formally recommended for consideration by the U. S. National Committee of the International Union of Pure and Applied Physics (I.P.U.) at Chicago, in June, 1933,[7] and also by the Electric and Magnetic Units and Magnitudes (E.M.M.U.) Committee of the I.E.C., at Paris,[8] in October, 1933.

At its recent plenary Holland-Belgium meeting, the I.E.C. found that none of its national committees, after examining the Giorgi system, were opposed to its adoption, while the delegates from fourteen countries were (with one abstention), unanimously in its favor. The I.E.C. therefore adopted the M.K.S. system with certain reservations; namely:

(*a*) It was recognized that four fundamental units are needed to complete the basis of the system; because on the basis of the M, K and S units, it would be possible to construct a number of electromagnetic systems to the exclusion of the practical volt-ampere-ohm series. The missing fourth unit might be selected from among the nine practical units of that series. The choice of the fourth fundamental unit was deferred until an opportunity had been offered to consult the opinions of the Symbols, Units and Nomenclature Committee (S.U.N.) of the I.P.U. and also of the Comité Consultatif d'Electricité (C.C.E.) of the Comité International des Poids et Mesures of Sèvres. Meanwhile, it was recognized that the study and use of the M.K.S. system could go on uninterruptedly, without waiting for the formal adoption of the fourth fundamental unit.

(*b*) Two countries made reservations on the question of retaining the *kilogram* as one of the four fundamental units. This is a theoretical question which does not affect the practical adoption and use of the M.K.S. system.

(*c*) The question as to whether the new system should be "rationalized" or "nonrationalized" was left undetermined for the present. It was recognized that much difference of opinion exists on this question; not only among the different countries in the I.E.C.; but also among different writers in each country. After sufficient time may have elapsed to permit opinions to crystallize and unify, it may be possible to reach an international decision. In the mean time, it is optional for any writer to adopt either "rational" formulas, following the lead of the Gaussian and Heaviside-Lorentz C.G.S. systems, or nonrational formulas, following the lead of the classical C.G.S. systems of Maxwell.

It is, however, agreed that whether the units and formulas selected by a writer are "rational" or "nonrational," the M.K.S.?. system is a single electromagnetic system, and that there is no need for a pair of parallel electrostatic and magnetic subsystems, as in the classical C.G.S. system. Every physical quantity should be represented in the M.K.S.?. system by one and only one unit. On the other hand, the M.K.S.?. system leaves the various existing C.G.S. systems entirely undisturbed; so that while the new system offers a great simplification to all students of electro-technics, it adds no new burden to students of physics.

In the future, it seems likely that new units belonging to the C.G.S. system will be open to the reception of impersonal names, if desired, like the *erg, dyne, phot,* etc. On the other hand, new units belonging to the M.K.S. system will be open to the reception of personal names, if desired, like the *ohm, volt, ampere,* etc. A temporary incongruity was unfortunately brought about by the International Electrical Congress of Chicago, in 1893, which passed a resolution that all practical magnetic units should be kept within the C.G.S. system. This led to personal names being adopted for certain C.G.S. magnetic units; the *gilbert, oersted, maxwell* and *gauss;* but it is to be hoped that with time and good-will, these exceptions can be ultimately cleared up.

The following table contains an incomplete list of M.K.S. units:

TABLE 1

M.K.S. UNITS AND THEIR CORRESPONDING C.G.S. UNITS

NO.	QUANTITY	SYMBOL	M.K.S.U.	C.G.S.U.	C.G.S.U. IN ONE M.K.S.U.	M.K.S.U. IN ONE C.G.S.U.
Mechanic						
1	Length	L	meter	centimeter	10^2	10^{-2}
2	Mass	M	Kilogram	gram	10^3	10^{-3}
3	Time	T	second	second	1	1
4	Area	S	m.^{2}	cm.^{2}	10^4	10^{-4}
5	Volume	V	m.^{3}	cm.^{3}	10^6	10^{-6}
6	Frequency	f	hertz, cy./sec.	cy./sec., hertz	1	1
7	Density	d	kg./m.^{3}	g./cm.^{2}	10^{-3}	10^3
8	Specific gravity		numeric	numeric	1	1
9	Velocity	v	m./sec.	cm./sec.	10^2	10^{-2}
10	Slowness		sec./m.	sec./cm.	10^{-2}	10^2
11	Acceleration	a	m./sec.^{2}	cm./sec.^{2}	10^2	10^{-2}
12	Force	F	joule/m.	dyne	10^5	10^{-5}
13	Pressure	p	joule/m.^{3}	barye	10	10^{-1}
14	Angle	α, β	radian	radian	1	1
15	Ang. velocity	ω	rad./sec.	rad./sec.	1	1
16	Torque	τ	joule/radian	dyne $\perp$ cm.	10^7	10^{-7}
17	Moment of inertia	J	kg. m.^{2}	g. cm.^{2}	10^7	10^{-7}

Energetic						
18	Work or energy	W	joule	erg	10^{7}	10^{-7}
19	Angular work $\tau\beta$	W	joule	erg	10^{7}	10^{-7}
20	Volume energy	w	joule/m.^{3}	erg/cm.^{3}	10	10^{-1}
21	Active power	P	watt	erg/sec.	10^{7}	10^{-7}
22	Reactive power	jQ	var	——	10^{7}	10^{-7}
23	Vector power		watt $\angle$	——	10^{7}	10^{-7}
Thermal						
24	Quantity	H	kg. calorie	g. calorie	10^{3}	10^{-3}
25	Temperature	θ	°C. or °K.	°C. or °K.	1	1
Luminous						
26	Luminous flux	ψ	lumen	lumen	1	1
27	Illumination	E	lux	phot	10^{-3}	10^{3}
28	Brightness	b	candle/m.^{2}	stilb	10^{-4}	10^{4}
29	Focal power	f	diopter	——	10^{-3}	10^{3}
Electric						
30	E.m.f.	E	volt	——	10^{8}	10^{-8}
31	Pot. gradient	H_e	volt/m.	——	10^{6}	10^{-6}
32	Resistance	R	ohm	——	10^{9}	10^{-9}
33	Resistivity	ρ	ohm.meter	——	10^{11}	10^{-11}
34	Conductance	G	mho, siemens	——	10^{-9}	10^{9}
35	Conductivity	γ	mho/m., siemens/m.	——	10^{-11}	10^{11}
36	Reactance	jX	ohm	——	10^{9}	10^{-9}
37	Impedance	Z	ohm $\angle$	——	10^{9}	10^{-9}
38	Quantity	Q	coulomb	——	10^{-1}	10^{1}
39	Displacement	Q	coulomb	——	10^{-1}	10^{1}
40	Current	I	ampere	——	10^{-1}	10^{1}
41	Current density	i	ampere/m.^{2}	——	10^{-5}	10^{5}
42	Capacitance	C	farad	——	10^{-9}	10^{9}
43	Spec. ind. capy.	ϵ/ϵ_0	numeric	numeric	1	1
Magnetic						
44	Flux	Φ	weber	maxwell	10^{8}	10^{-8}
45	Flux density	B	weber/m.^{2}	gauss	10^{4}	10^{-4}
46	Inductance	L	henry	——	10^{9}	10^{-9}
47	Rel. permeability	μ/μ_0	numeric	numeric	1	1

Table 2 lists the principal units of the M.K.S. system which are affected by the principle of "rationalization." The table shows that the rationalized units are already furnished with international names; although some of them are cumbersome and may perhaps be replaced by new shorter names in the future. None of the unrationalized units appear, as yet, to have international names. It might be possible to use the names *pragilbert* and *praoersted* for Nos. 51 and 52 nonrationalized; but the prefix *pra*, suggested at the I.E.C. meeting of Stockholm, in 1930, has met with but little international support up to the present time.

TABLE 2

M.M.S. SYSTEM ELECTRIC AND MAGNETIC UNITS CHANGED BY RATIONALIZATION

NO.	QUANTITY	SYMBOL	NAME OF M.K.S. UNIT RATIONALIZED	NAME OF M.K.S. UNIT UNRATIONALIZED	NO. OF UNRAT. U. IN ONE RAT. U.
Electric					
48	Electric flux	ψ	coulomb	——	
49	Flux density	D	coulomb/m.^{2}	——	
50	Space inductivity	ϵ_0	farad/m.	——	
50a*	Num. value of ϵ_0		$10^7/4\pi c^2 = 8.854 \times 10^{-12}$	$10^7/c^2 = 1.113 \times 10^{-10}$	
Magnetic					
51	Magnetomotive force	$\mathfrak{F}$ or M	ampere-turn	——	4π
52	Potential gradient	H	amp.-turn/m.	——	4π
53	Space permeability	μ_0	henry/m.	——	$1/4\pi$
54*	Num. value of μ_0		$4\pi \times 10^{-7} = 1.257 \times 10^{-6}$	10^{-7}	
55	Space reluctivity	υ_0	m./henry	——	4π
56	Num. value of υ_0		$10^7/4\pi = 7.958 \times 10^5$	10^7	
57	Permeance	$\mathfrak{P}$	weber/amp.-turn	——	$1/4\pi$
58	Reluctance	$\mathfrak{R}$	amp.-turn/weber	——	4π
59	Pole strength	m	weber	——	$1/4\pi$
60	Magnetic moment	$\mathfrak{M}$	weber.meter	——	$1/4\pi$
61	Magnetization	$\mathfrak{J}$	weber/m.^{2}	——	$1/4\pi$

* Owing to admitted small discrepancies of a few parts per myriad, between certain existing practical unit standards and their absolute theoretical values, the future adoption of a fourth fundamental M.K.S. unit might slightly alter[9] these numerical "constants." In 50a, the transmission velocity c is taken as 2.998×10^8 m./sec.

* Equivalent to 10^{-7} unrationalized.

[1] International Congress of Electricians, Paris, 1881, Resolutions.

[2] *Proc. Int. Elec. Cong. Chicago*, Chamber of Delegates (1893).

[3] *Proc. Int. Elec. Commission* (1906–1935).

[4] J. Clerk-Maxwell, "A Treatise on Electricity and Magnetism" (1881).

[5] G. Giorgi, "Unità Razionali di Elettromagnetismo," *Atti dell A.E.I.* (1901).

[6] G. Giorgi, "Proposals Concerning Electrical and Physical Units," *Trans. Int. Elec. Cong. St. Louis*, **1**, 136–141 (1904).

[7] *Bull. Natl. Res. Coun.*, No. **93**, 1933, *Int. Union Pure and Applied Physics*, Chicago, p. 2.

[8] I.E.C. Document R.M. 105, Meeting of E.M.M.U. Subcommittee, Paris, Oct., 1933.

[9] I. E. C. Document, June, 1934, "Memorandum on the M. K. S. System of Practical Units" by G. Giorgi.

PRELIMINARY REPORT ON THE PROBABLE CONNECTION BETWEEN THE BLOOD GLAND AND THE CHROMATOPHORE ACTIVATOR IN DECAPOD CRUSTACEANS

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Communicated August 19, 1935

During my investigations of the nervous system and the sense organs of crustaceans (1931–1935) I have found two organs, the blood gland and the *X*-organ, which on account of their cytology must be regarded as incretory in function. They usually lie in the eye-stalks and are innervated from the medulla terminalis. Owing to the structure, the situation in the eye-stalks and the innervation from a part of the brain, that is intimately connected with the optic paths, I have advanced the hypothesis, that the said organs might be the source of the substance, found by Perkins (1928) and by Koller (1928) to be responsible for the concentration of the pigment within the chromatophores of the skin, or—which is also probable—with the pigment adaptation of the compound eyes, a process also influenced by incretory means (Welsh, 1930). In order to test this hypothesis I have during the summer of 1935 made extracts of the eye-stalks and heads of numerous decapod crustaceans, which are found in the vicinity of the Marine Biological Laboratory at Woods Hole, simultaneously with a study of the anatomy of the same organs by means of sectioning and staining.

Of the 16 species of higher crustaceans, which were formerly investigated by different authors (compare Kropp-Perkins, 1933), I have tried the following: Palæmonetes vulgaris, Homarus americanus, Cancer irroratus and Callinectes sapsidus, and thus am able to confirm the statements of Perkins regarding the occurrence of a chromatophore activator in the eye-stalks of these decapods. In addition I have found the same substance present in extracts from the following decapods: Crago (Crangon) vulgaris, Leander tenuicornis, Cambarus sp., Pagurus pollicaris, Gebia affinis, Hippa talpoidea, Carcinus granulatus (moænas), Cancer borealis Libinia dubia, Ovalipes ocellatus and Panopæus sayi. In this connection it is interesting to note that in Cambarus, the only fresh-water form thus far investigated, the extract from the eye-stalks does not reach its complete capacity until it has been boiled. In all cases Palæmonetes and sometimes Crago and Uca pugilator too were used as test animals.

In all decapods thus far investigated by me, except Gebia and Hippa, the substance, which concentrates the red and yellow pigment in the chromatophores of the skin, is found in extracts from the eye-stalks, whereas the same substance in Gebia and Hippa is found in extracts from the head, their eye-stalks being totally inactive in this respect. During a micro-

scopic examination of the eye-stalks and the heads of the decapods thus investigated there was found a significant connection between the position of the blood gland and the *X*-organ, which both usually lie in the neighborhood of one another, and the position of the source of the pigment concentrating substance. Thus in all the said crustaceans except Gebia and Hippa both incretory organs lie in the eye-stalks, whereas in Gebia and Hippa they lie in the head on the surface of the brain.

Experiments were also carried out in order to investigate the position of the source of the pigment concentrating substance within the eye-stalks of those crustaceans in which the eye-stalks are the activating organs. Then it was found that, for instance in Callinectes, the distal-dorsal half of the eye-stalk contains the active substance and both the incretory organs, in Homarus on the contrary the proximal half is the seat of these organs. In Pagurus the activator comes from the two proximal thirds and in Uca pugilator, according to experiments made by Dr. Sven Carlsson, who for two months was working in coöperation with me at Woods Hole, the middle third of the eye-stalk is the active center. Now in Uca the middle third of the eye-stalk contains the blood gland, which is well developed, whereas the *X*-organ either is very small or perhaps completely reduced. In Pagurus finally the sections made of different parts of the eye-stalks show that the blood gland, that usually is a more or less round or oval body, has a special form and is very long, so that it reaches through both the proximal and the middle thirds of the eye-stalk. The *X*-organ of Pagurus is situated in the proximal third, which thus contains part of the blood gland and the whole *X*-organ. Since the middle third of the eye-stalk of Pagurus, that contains only part (the larger part, however) of the blood gland, concentrates as least as strongly the red and yellow pigment as the proximal third does, this fact in connection with those earlier mentioned tells in favor of the theory that the blood gland is the real source of the pigment concentrating substance in the decapod crustaceans. I wish, however, to state that my experiments do not show that the *X*-organ would not at all be connected with the color changes of the crustaceans, especially as Parker (1932) and Brown (1933) have maintained that there ought to be more than one hormone connected with the changes of the skin pigment. According to Brown one hormone concentrates the red and yellow pigment and another the white. Besides there seems to be ample opportunity for hormone activity in the crustaceans as for instance in connection with the pigment adaptation of the eyes (Welsh, 1930), the calcium metabolism (Koller, 1930), and the growth promoting action found by Navez and Kropp (1934).

The full paper on this subject will probably be published toward the end of 1936.